THE STRUCTURE AND SOME ASPECTS OF DEVELOPMENT OF THE ONYCHOPHORAN HEAD

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The position of *Peripatus* relative to the arthropods on the one hand and to the annelids on the other has led to an amount of attention paid to this animal all out of proportion to its inoffensive, retiring, and unspectacular habits. The reasons for this attention are not difficult to understand when one considers that it apparently represents a link between two very important phyla.

The characters wherein *Peripatus* appears to be close to the arthropods are striking and significant. The body wall is similar to that of many arthropods. The appendages diverge from the chaetal type found in the annelids and exhibit more the embryological and later developmental growth found in the arthropods. In fact, Snodgrass (1938) considers the walking leg of *Peripatus* to be the prototype of the arthropod limb.

Peripatus has on the other hand definite relationships with the annelids. It is wormlike with no distinct body regions. In the adult stage it has no definitely segmented areas, though it has a head region distinct in function from the rest of the body. Internally the nerve cord is distinctly similar to the annelid type, though the anterior end, especially the brain, shows some advances in structure.

Internally, the alimentary canal, especially in the anterior end and the middle sections, and the peritrophic membrane, especially in its origin, are strikingly similar to those of the insects. The heart also exhibits the more simplified form found in insects and in some other arthropods. Is it any wonder, then, that over the long period of years during which workers have investigated this animal many of them have considered it to belong to the phylum Arthropoda?

I do not wish, within the limits of this paper, to make an extended study of the literature on *Peripatus*. That has been thoroughly done by several others, and those who wish to pursue that subject further I refer to the bibliographies in the works of Snodgrass, Manton, and Weber.

Any work in connection with the head of an invertebrate such as *Peripatus* inevitably must include a discussion of segmentation. Of the many workers who have applied themselves to this problem there are several who in late years have either contributed original data as a result of their own research or have written compilations that are extremely valuable to the anatomist. Of these workers, Federov (1929) alone of the group confined himself to a single organ system of the adult in his two extensive papers on the nervous system of *Peripatus tholloni*. Realizing the importance of the nervous system as a criterion of segmentation, he tried to identify segmental areas in the ventral nerve chain of the animal and to correlate the cerebral nerves with the nerves of these segmental areas.

Pflugfelder (1948) in a paper on the embryology of *Paraperipatus amboinensis* comes to conclusions concerning head segmentation that support Federov's ideas. Pflugfelder, however, was handicapped by the fact that he apparently considered the jaws of *Peripatus* to correspond to the mandibles of the arthropods, and he formulated his arguments to prove this point, a fact which I think limits the value of his work.

Manton in a series of papers published after 1938 has given very valuable accounts of the embryology, anatomy, and habits of *Peripatus*. But her work on embryology was mainly concerned with the thesis that segmentation is instigated by the mesoderm and that in this respect the nervous system is of little importance. More will be said about the work of these two later in this paper.

Snodgrass, in his paper of 1938 on the Annelida, Onychophora, and Arthropoda, gave a remarkably clear and complete description of the development and anatomy of this animal.

Weber, in his "Morphologie, Histologie und Entwicklungsgeschichte der Articulaten" published in 1952, devoted a lengthy section to the Onychophora in which he compared the ideas of L. M. Henry (1948) to those of Pflugfelder published the same year. He agrees with Pflugfelder's opinion that the jaws of the Onychophora are the true mandibles as opposed to Henry's statement that they belong to the tritocerebral segment. In his paper Weber quotes Pflugfelder at length in regard to principles to be followed in homologizing organs in different groups of animals. He says, "Care must be taken not to homologize in all details the tritocerebrum of the Onychophora and the stomatogastric nerves emanating therefrom with the tritocerebrum of the Arthropoda on the one hand and the corresponding parts of the nervous system of Annelida on the other. The Onychophora do not

represent a conglomerate of characteristics of Arthropoda and Annelida but despite the apparent mixture of characteristics of both animal groups, they represent harmonious animals in which individual differences are present."

Pflugfelder makes this statement after discussing the relationship of the first postoral commisure to the "jaws" or, as he considers them, the "mandibles." I agree that one should be careful in forming homologies, but the same principles apply to the mandibles themselves, and in regard to these very important organs Pflugfelder is so convinced that the onychophoran "jaws" are true mandibles, that he interpolates what I consider to be an entirely imaginary ventral organ and ganglion between the mandibles and the antennae in order to provide a "premandibular" segment in the Onychophora that will be homologous with the premandibular segment of the arthropods.

My purpose in undertaking this research problem was to make a thorough anatomical study of the head region and particularly the "jaws" and then to review the embryonic development of the head to see if a different interpretation would be justified. The form used for the dissections in this study was *Peripatoides novae-zealandiae* (Hutton).

The head of *Peripatus* (fig. 1 A) is an undifferentiated region of the body, unmarked by sutures or grooves that would give any clues as to its limits or segmental areas. The antennae (*Ant*) are large and are situated on the extreme anterior end on the dorsal side. Beneath them and slightly caudad are the inconspicuous eyes and the opening into the preoral cavity (*Pcav*). This cavity is ringed with lobes that form lips which when pressed together effectively close the mouth. Deeply enclosed within the preoral cavity are the feeding claws (*Fcl*), with only their tips exposed in the preoral opening. The first pair of appendages behind the mouth are the slime papillae (*Slp*) called by some investigators the oral papillae, and behind them are the first pair of legs.

A series of parasagittal dissections will indicate the limits of the preoral cavity and its relation to the real mouth opening which lies within the cavity itself (fig. 2 A, B, C, D). In preparation for A, the head surface was removed on the dorsal side, revealing the brain (*Br*) and the circumoral folds (*Cof*). In this figure the two teeth of the right feeding claw (*Fcl*) are prominent.

The walls of the preoral cavity are deeply folded in such a way that the lobes (*Dl*) formed between these folds are arranged radially and extend onto the outer surface of the body (figs. 1 A, 2 A).

In the dorsal wall of the preoral cavity there is located an enlarged lobe called by Snodgrass the "labral lobe" but by Manton and others the "tongue" (figs. 1 A, 2 A, *Dl*). Though this structure appears to be independent of the ring of lobes around the edge of the opening, I believe that it is simply one of the circumoral lobes greatly enlarged
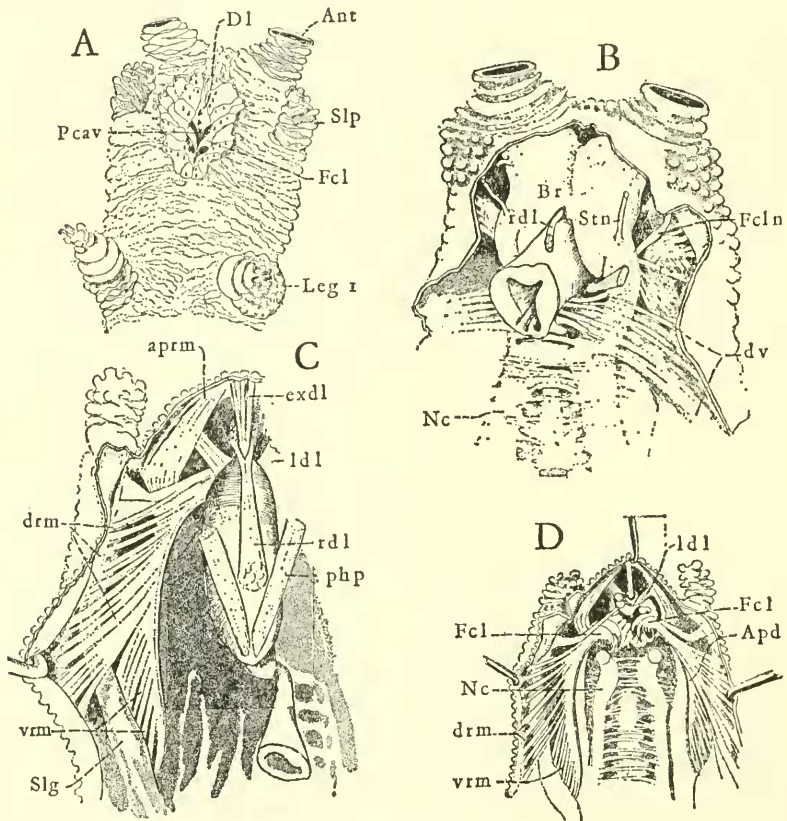

FIG. 1.—Onychophora. Internal structure of the head of *Peripatoides novae-zealandiae.*

A, head from ventral side. B, dorsal dissection of head showing brain and associated structures. C, same with brain removed. D, same with brain and oesophagus removed.

Ant, antenna; *Apd,* apodeme of feeding claws; *Fcl,* feeding claws; *Fcln,* feeding claw nerve; *Dl,* dorsal lobe; *Br,* brain; *Nc,* ventral nerve cord; *Pcav,* preoral cavity; *Slp,* slime or oral papillae; *Slg,* slime gland; *aprm,* anterior protractor muscles of the feeding claws; *drm,* dorsal retractors of the feeding claws; *dv,* dorsoventral muscles; *exdl,* anterior extensor muscles of the dorsal lobe; *ldl,* lateral dilators of dorsal lobe; *php,* protractor muscles of pharynx; *rdl,* retractor muscle of dorsal lobe; *vrm,* ventral retractors of feeding claws.

to form an organ to help in the swallowing of food. Though it is equipped with powerful muscles and has a row of external spines, in these respects resembling somewhat the epipharynx of some insects, it cannot in any way be considered as a labrum. Neither is it a tongue in the sense that the hypopharynx of chewing insects is a tongue. It simply is one of the circumoral ring of lobes, though much larger than
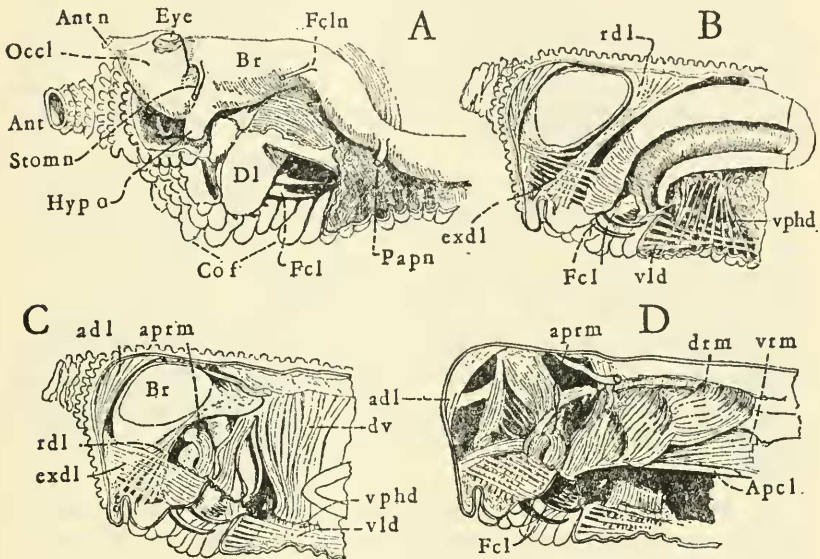

FIG. 2.—Lateral dissections of the head.

A, vertical dissection with brain in place, dorsal body wall removed. B, median dissection with brain cut. C, same with oesophagus removed. D, same with brain removed.

Antn, antennal nerve; *Apcl,* apodeme of feeding claws; *Br,* brain; *Cof,* circumoral folds; *Fcl,* feeding claws; *Fcln,* nerve of feeding claw; *Hypo,* Hypocerebral organs; *Occl,* occular lobe; *Papn,* papillar nerve; *adl,* anterior dilators of the oral lobes; *aprm,* anterior protractors of the feeding claws; *exdl,* anterior extensors of the dorsal lobe; *drm,* dorsal retractors of the feeding claws; *dv,* dorsoventral muscles; *vld,* ventral longitudinal dilators of the oral lobes; *vphd,* ventral dilators of the oesophagus; *vrm,* ventral retractors of the feeding claws.

any others in the preoral cavity, and is here called the dorsal lobe (*Dl*).

Now let us examine this structure more closely. When the mouth is closed it is apparent that this dorsal lobe closes the opening by fitting tightly within the circle of other lobes. When the animal relaxes the muscles of the mouth region, the mouth opens wide and the dorsal lobe may be pushed out and retracted. The spines on its lower keel-

like edge, though small, are slanted backward, and it is apparent that they aid in pushing food back into the oesophagus.

A dorsal dissection indicates that there are two sets of muscles concerned with the movement of this lobe (fig. 1 C). They are:

1. The anterior extensor of the dorsal lobe; a bundle of several fibers arising on the anterior head wall and inserted on the wall of the oesophagus where the lobe joins the oesophagus (fig. 1 C, D, *exdl*).

2. The median retractor of the dorsal lobe; a large muscle bundle attached to the dorsal body wall, extending forward where it forks to pass around the anterior extensors of the dorsal lobe, each branch being inserted on the posterior median wall of the dorsal lobe (fig. 1 C, *rdl*).

Laterad of the retractor of the dorsal lobe there are two diagonal muscles which, though not attached directly to the base of the lobe, are closely associated with muscles 1 and 2 and have considerable effect on the functioning of the lobe. They are:

3. The lateral dilators of the pharynx originating on the body wall, passing inward underneath the anterior protractors of the feeding claws (*aprm*) to their insertions on either side of the oesophagus. These muscles resist the pull of the median retractors and are in turn opposed by the action of the circular muscles of the oesophagus (fig. 1 C, D, *ldl*).

On the anterior surface of the head there is a group of muscles directly concerned with the opening and closing of the preoral cavity. These muscles are:

4. The anterior dilators of the preoral lobes; muscle fibers arising dorsad on the front of the head; inserted at the base of the lobes at each side of the median dorsal lobe (fig. 2, B, C, D, *adl*).

Other muscles concerned with the swallowing of food, though they are not actually attached to the oral lobes, are the following:

5. The ventral pharyngeal dilators. These are vertical muscles consisting of distinct fiber bundles originating on the ventral median body wall and inserted dorsally on the underside of the oesophagus (fig. 2 B, C, D, *vphd*).

Several groups of muscles in the head consist of flattened fibers lying in sheets close to the body wall. These sheets are very thin and appear almost membranous. These are:

6. Ventral longitudinal dilators of the oral lobes. These are divided into two bands originating on the ventral body wall, extending forward, one band on each side of the ventral pharyngeal dilators and inserted in the walls of the ventral posterior oral lobes (fig. 2 B, C, D, fig. 3 A, *vld*).

7. Lateral dilators of the oral lobes; large flat sheets of muscles originating on the body wall near the bases of the antennae; inserted in the large lobes adjoining the median dorsal lobe (fig. 3 A, *ldm*).

8. Lateral sphincter muscles of the oral lobes. These are large sheets originating on the anterior head wall; inserted ventrally and
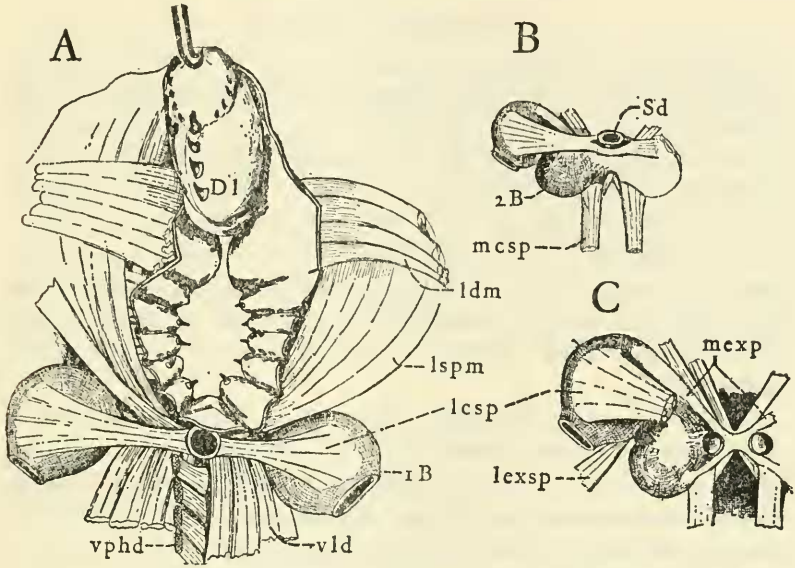

FIG. 3.—Dissections of the oral lobes, and the salivary pump.

A, dorsal dissection with inner wall of preoral cavity removed showing salivary pump. B, salivary pump with ventral muscle sheet removed to expose the entire salivary pump. C, same dissection with the median salivary duct removed.

1B, outer lobe of salivary pump; *2B*, inner lobe of salivary pump; *Dl*, dorsal lobe; *Sd*, salivary duct; *lcsp*, lateral compressors of salivary pump; *ldm*, lateral dilators of the oral lobes; *lcxsp*, lateral extensors of the salivary pump; *lspm*, lateral sphincter of the oral lobes; *mcsp*, median compressors of salivary pump; *mexp*, median extensors of salivary pump; *vld*, ventral longitudinal dilators of the oral lobes; *vphd*, ventral dilators of the oesophagus.

posteriorly in the oral lobes near the insertions of the ventral longitudinal dilators of the oral lobes (fig. 3 A, *lspm*).

These muscles lie exterior to the lateral dilators of the dorsal lobes and, when contracted, pull the ventral oral lobes together, thus helping to close the mouth.

Other small sheets of muscles not shown in the figures for this paper lie near the body wall and are inserted in the lobes, apparently just a few fibers to each lobe. Some of these lie underneath the lateral sphincter muscles and are inserted in the lateral oral lobes much as

are the lateral dilator muscles. Others lie beneath the ventral longitudinal dilators and function in a similar fashion to those muscles. Since these small sheets of muscles have the same apparent function as the larger muscles with similar insertions that are adjacent to them, they are not assigned separate numbers in this list.

THE SALIVARY GLANDS

A dissection in which the alimentary canal is removed and the mouth and preoral cavity are arranged so that one, in examining the preparation, looks out the mouth opening (fig. 3 A), reveals not only the musculature of the oral lobes very clearly, but also indicates that the salivary ducts are formed into a series of complicated folds that form very effective valves. Each salivary gland empties into a button-shaped chamber (*1B*) lying laterad of the ventral longitudinal sheet of muscles (*vld*). The common salivary duct (*Sd*) lying between these chambers is connected to each chamber by narrow bands of muscles, each band fanning out distally where it inserts on the chamber (*lcsp*).

When the ventral longitudinal sheets of muscles are removed, a second swelling in each lateral duct is revealed lying mesad and slightly underneath the first chamber (figs. 3 B, C, 2 B). These chambers form not only an effective salivary pump but also the valves that are so necessary in the operation of such a pump.

The muscles that operate the pump and valves are as follows:

9. The paired lateral compressors of the salivary pump originating on the walls of the median salivary duct; inserted on the outer chamber (fig. 3 A, B, *lcsp*). These muscles by their contraction close the valve between the pump and the salivary gland when the salivary juice is being ejected from the common duct into the preoral cavity.

10. The median compressors of the salivary pump. A pair of longitudinal muscles lying near the center line originating on the body wall and inserted on the inner edge of the inner chamber of the pump (fig. 3 B, C, *mcsp*). These muscles when contracted prevent a twisting movement of the lateral ducts, thus aiding in the closing of the passage between the two chambers.

The compressor muscles are opposed in their action by several small muscles that, when they contract, together open the passage between the two chambers. They are:

11. The lateral extensors of the salivary pump. Each muscle of this pair is attached distally to the body wall and medially to the inner edge of the outer chamber (fig. 3 C, *lexsp*).

12. The median extensors of the salivary pump. A group of small muscles that are intimately associated with the small muscles under 6 (*vld*). They appear to form an X underneath the common duct where they attach to the body wall. Distally they insert along the edges of the inner chamber, one anterior to the duct, the other posterior to the duct on each side (fig. 3 C, *mexp*).

The action of these muscles together with the lateral extensors apparently straightens out the two chambers on each side, thus opening up the passage between them; in other words, they open the valve.

Many other small fibers already assigned to muscle *vld* converge on the center line at the same point. Others of this group lie on top of the inner chambers and appear by their action to compress the inner chambers. I did not find any other valve mechanism that would prevent liquid from reentering the ducts when the compressor muscles are relaxed. It may be that the action of the longitudinal muscles just mentioned would accomplish this purpose by forcing the median chambers closed when the lateral chambers are extended by the relaxation of muscles 11 and 12.

THE FEEDING CLAWS

The "jaws" of *Peripatus* consist each of a pair of long, slender claws (figs. 1 D, *Fcl*) protruding into the oral cavity from their bases which are deeply invaginated within the body (figs. 1 A, 2 A, B). Only their tips are to be seen lying across the mouth opening. From their inner ends long apodemes (*Apd*) extend into the body cavity, and to these, powerful muscles are attached. The muscles are capable of acting as protractors or retractors, the retractor muscles also acting as flexors of the claws. These organs have been the subject of a great deal of investigation, and many views have been presented as to their segmental relationships. Some German workers apparently have been convinced not only that they are true jaws but that they are homologous with the mandibles of the arthropods. However, though they lie almost in the same plane, they are not opposed to each other and in fact do not in the least act as true jaws. They are not crushers or chewers of food but they act instead as claws or rakes with which the animal simply scratches particles of food away from the food source so that other mechanisms of the ingestive apparatus are able to move them into the mouth in a position to be swallowed.

Further comparison with the arthropod mandible reveals pertinent facts which may give us a clue in identifying the segment to which

they belong. In the arthropods, though the appendages constituting the mouth parts of chewing forms are considered to be modified legs, the actual working structures of the mandibles, maxillae, and the labium where one is present, are formed from endite lobes of the two basal segments of the telopodite according to Snodgrass (1935). The telopodite becomes reduced and acts as a sensory organ or, in the case of the mandibles, is lost entirely.

Though appendages of both the Onychophora and the Arthropoda have had a common origin as lobiform outgrowths of the body wall, nothing like the elaborate development of the leg of arthropods takes place in the Onychophora. The differentiation of the onychophoran leg into a thick basal part and a slender distal part, as Snodgrass says (1938), might be seen as an incipient segmentation, but the development of endite lobes on the basal leg segments of arthropods into the chewing and crushing structures we call mandibles finds no parallel development in the Onychophora.

The "jaws" of *Peripatus* are simply the claws at the end of the appendage, greatly enlarged when compared with the claws of the walking legs but not greatly different from them in function. Tiegs (1949) recognized this when he said that the "jaws" of *Peripatus* were merely enlarged claws. Also they are not retracted simultaneously as are the mandibles of a chewing insect for example, but are retracted alternately, according to Manton (1937). For these reasons the term "jaws," though firmly established in the literature, is incorrect, and the organs should be designated as the "feeding claws."

To understand how these claws work one must consider them as the tip ends of greatly strengthened legs which have been withdrawn into the body so that just the tips of the claws project into the oral cavity (figs. 1 A, 2 A, B, C, D). The muscles then taking them from the anterior to the posterior consist of the following groups:

13. Anterior protractor of the claws (fig. 1 C, D, *aprm*), a powerful group of muscles arising anteriorly on the head wall and inserted at the base of the claws. (The apparent distortion of these muscles indicated in the sketch is probably due to stresses put upon them by the hooks holding the dissection in place.)

14. The dorsal retractor of the claws (*drm*) consisting of widely spaced fibers originating on the body wall above the slime gland ducts; inserted on the retractor apodeme of the claw. These muscles correspond to branches, a, b, c, d, and e of the retractor of the claws as described by Calora (1957).

15. The ventral retractors of the claws (*vrm*); a broad fan of

muscles originating caudad of 13 on the body wall but below the slime gland duct and inserted on the retractor apodeme.

Such evidence concerning the homologies of the feeding claws as given above would be inconclusive were it not supported by the evidence of embryonic development. Here, too, investigators who have worked on the development of this form are in disagreement. Unfortunately no material was available for a study of this kind. Consequently one must rely on the works of others for information on head development. Of those who have published on the embryology of *Peripatus,* Pflugfelder (1948) and Manton (1949) have worked most recently, and it is mainly from their papers that the following account has been taken.

DEVELOPMENT OF THE EMBRYO

The entoderm and mesoderm of *Paraperipatus amboinensis* originate separately from cells proliferating inwardly from the ventral part of the blastoderm according to Pflugfelder. The entoderm appears first and forms in a short time an inner lining which becomes one cell in thickness except where the cells bunch up at the zone of proliferation (fig. 4 E, *Ent*). This point of proliferation is flanked by tall, slender cells known as fibroid cells (*Fz*). A groove forms beneath this zone in the early gastrula stage which Pflugfelder calls the primitive groove. He purposely avoids the term "blastopore," for he says, "such a porus appears nowhere during the fetal development of *Paraperipatus amboinensis.*" This groove apparently corresponds to the early transient blastopore noted by Manton. The development of the endoderm continues long after the majority of coelomic pouches have appeared (fig. 4 G).

The formation of the mesoderm, like the formation of the entoderm, takes place at a spot closely behind the primitive cavity, being formed from the beginning in pairs. The right and left immigrating zones are separated by median fibrous cells (fig. 4 F). At the points of proliferation, the cells accumulate as domelike invaginations, but laterally they thin out into single cell layers which push between the entoderm and the ectoderm (fig. 4 F, *Mes (lat)*). Even in these dome-like masses the cells have a tendency to arrange themselves into a single layer which causes the coelomic cavities to form (*Coel*).

An undifferentiated mesodermal band does not appear in the head region in front of the primitive cavity; the immigrated mesodermal material rather differentiates close to its place of origin into the paired coelomic pouches and into the further proliferating lateral mesoderm.
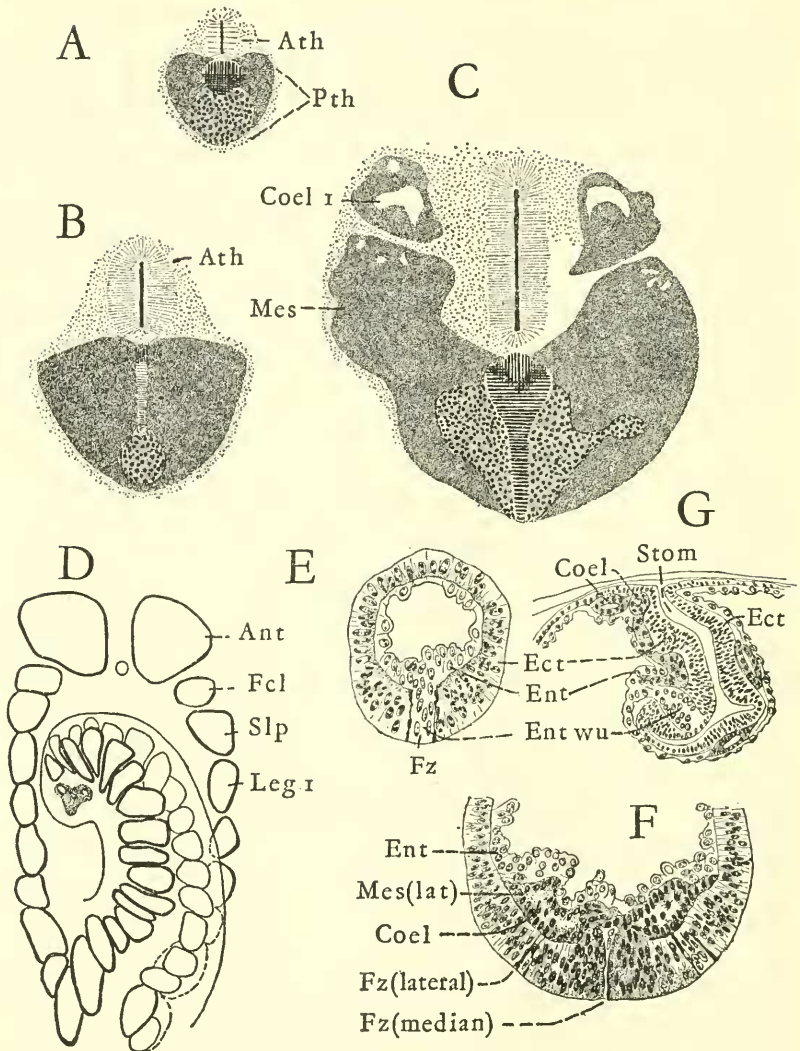
FIG. 4.—Embryonic development of endoderm and mesoderm.

A, B, C, 3 stages of the development of germinal disc of *Peripatopsis mosleyi* (adapted from Manton). D, late stage in development of coelomic sacs, *Peripatopsis mosleyi* (adapted from Manton). E, F, G, stages in development of mesoderm and endoderm in *Paraperipatus amboinensis* (adapted from Pflugfelder).

Ant, coelomic sacs of antennal segment; *Ath,* anterior thickening (Manton); *Coel,* coelomic cavities; *Ect,* ectoderm; *Ent,* entoderm; *Entwu,* point of proliferation of entoderm (Pflugfelder); *Fcl,* coelomic sac of feeding claw segment; *Fz,* fiber cells (Pflugfelder); *Mes,* mesoderm; *Pth,* posterior thickening (Manton); *Slp,* coelomic sacs of slime papillae; *Stom,* stomodaeum.

Through the longitudinal growth of the ectoderm the coelomic pouches are passively removed from the place of their origin; i.e., from the very beginning they remain connected with that point of the germ band to which they belong functionally, according to Pflugfelder.

In some species the blastopore and thus also the point of proliferation of the mesoderm remain at the posterior end of the body. According to Manton, at the stage when the germ band forms on the surface of the blastoderm, two germinal discs occur, in various species of *Peripatopsis* worked on by her, as separate thickenings of the blastoderm. The posterior thickening (*Pth*) arises first, followed quickly by an anterior thickening (fig. 4 A, B, *Ath*). The posterior thickening (*Pth*) gives rise to the blastoporal area from which the mesoderm is formed in all species described by her, and from which in some species the entoderm is also formed. The anterior thickening gives rise to the ectodermal part of the lips of the mouth-anus (fig. 4 A, B, *Ath*) and later to the midventral ectoderm of the body.

The proliferating mesoderm forms a U, with the arms pushing in an anterior direction around the anterior thickening (fig. 4 C, *Mes*). When the arms reach the halfway mark along the mouth-anus, the anterior portions of each arm break away, become hollow, and form the coelomic sac of the first somite (fig. 4 C, *Coel* 1). As the arms continue to push forward, succeeding somites are formed in a like manner. In the meantime the groove forming the mouth-anus has elongated and the middle edges have grown together, leaving only the mouth and anal openings which become ever more widely separated as the embryo grows in length. Figure 4 D shows the embryo with the last pair of coelomic sacs separating from the mesodermal band, after which the mesodermal band soon disappears.

Manton says of the anterior sacs, "The first pair approach each other anterior to the mouth and establish the antennal segment. The second pair are smaller and lie at the side of the mouth where they establish the mandibular segment. The third pair are larger than the second and all succeeding somites in early stages in some species . . . and establish the slime papilla segment."

As for the development of the nerve cord we must turn to Sedgwick (1885), Kennel (1888), and to Pflugfelder, since Manton does not discuss this important phase of development in her paper. The nerve cord of *Paraperipatus amboinensis* according to Pflugfelder develops from paired thickenings on the ventral side of the embryo.

These ridges become segmented as the result of concentrations of ganglion cells, and the resultant lobes are known as the ventral organs.

Unfortunately Pflugfelder does not figure them in whole mounts in his paper, but Sedgwick (1885) for *Peripatus capensis,* and Kennel (1884, 1888) for *Peripatus edwardsi* and *Peripatus torquatus,* show the arrangement of the ventral organs very clearly from the ventral side. Figure 5 A of *Peripatus capensis* illustrates an early stage in the development of the ventral side of the embryo. In this figure, though the lips of the oral cavity are already forming, the appendages of the second visible segment which will become the feeding claws are still located laterally. Adjacent to them the lobes that will form the feeding claws are evident, and the relationship of the future feeding claws to this segment is unmistakable. In figure 5 B the lips have become much more extensive and the feeding claws have begun to withdraw into the preoral cavity and with them the ventral lobes of the second segment. The antennae and the antennal lobes are distinctive from the first, and the appendages of the segment following that of the feeding claws show by the presence of the forming orifice that they will become the slime glands. Figure 5 C shows the ventral organs lying adjacent to each other along the center line. The segments indicated in these three figures, therefore, are the antennal with the largest ventral lobes, the segment of the feeding claws with ventral organs that become much smaller as the embryo develops, and the segment of the slime glands.

Figure 5 D has been adapted from Kennel and shows a slightly later stage of *Peripatus edwardsi*. Here the feeding claws and the ventral lobes of the feeding claw segment have withdrawn completely into the oral cavity, the large anterior ventral lobes are the antennal lobes ; those immediately caudad of the preoral cavity are the lobes of the papillar segment. The large dorsal lobe of the oral lips is distinct in this figure.

At least at the time of their origin the ventral organs show a striking similarity to the developing neural ridges of some beetle embryos, as a study of these figures indicates. However, some significant differences soon appear. In the first place nerve cells do not form from neuroblasts in the ectoderm as in insects, but instead cells of the organs migrate through the inner "basement membrane" to form the nerve cord, and as they continue through the membrane, the ventral organ shrinks in size and finally disappears. Only those of the antennal segment are retained and appear on the under side of the adult brain as the hypocerebral organs (fig. 2 A).

According to Evans (1902) the brain also includes a pair of anterior archicerebral lobes belonging to the anterior extremity of the head, and Pflugfelder by means of serial sections was able to demon-

strate the presence of two widely spaced but much smaller ventral organs lying anterior to and underneath the antennal lobes. However, these anterior ventral organs apparently never reach a size suffi-
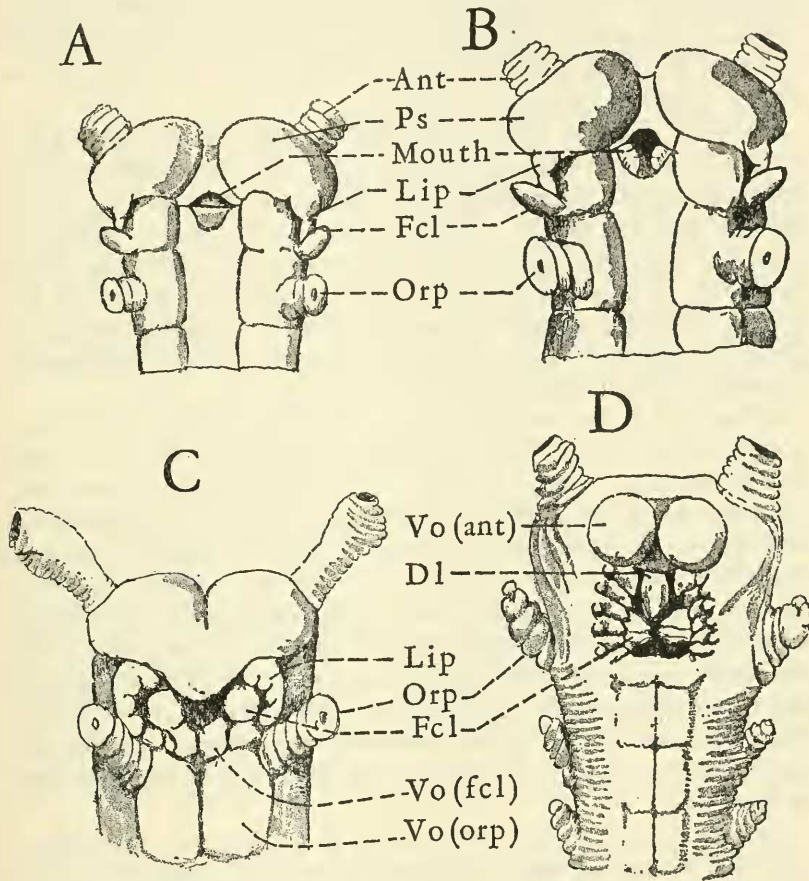

Fig. 5.—Development of onychophoran head.

A, B, C, stages in development of *Peripatus capensis,* adapted from Sedgwick. D, older embryo of *Peripatus edwardsi,* adapted from Kennel.

Ant, antenna; *Dl,* dorsal lobe; *Fcl,* feeding claw; *Orp,* oral papilla (Sedgwick); *Ps,* preoral somite (Sedgwick); *Vo,* ventral organ.

cient for them to be seen in whole mounts of the embryo, since they have not been reported by previous workers. Thus the brain appears to be composed of three ganglionic centers, the optic lobe, the antennal lobe, and a third pair of lobes with nerves given off to the stomodaeum and the feeding claws. According to Pflugfelder, Plate in 1922 recog-

nized this arrangement, and he further homologized the feeding claws with the second antennae of the Crustacea and the slime papillae with the mandibles of the Crustacea, the Myriopoda, and the Insecta. Such an interpretation of the third brain with its nerve connections running to the feeding claws is in accord with the opinions of many authors, among them being Manton (1949), Holmgren (1916), Hanström (1935), Henry (1948), and others.

However, Federov (1929) considers that the brain consists of the prostomial archicerebrum and of postoral elements consisting of the antennal centers, the premandibular centers, the mandibular centers, and the papillar centers. Snodgrass says of his work, "Federov's elaborate analysis of the brain structure and nerves would be more convincing if it took into account the embryonic development of the brain; his results are entirely unsupported by ontogenetic evidence, and are mostly at variance with observations on the brain development reported by other investigators."

Pflugfelder in his study on the development of *Paraperipatus amboinensis* gives considerable evidence in support of Federov's idea and illustrates his findings by a series of reconstructions of cross sections through the head region. The third or tritocerebral segment he considers to be anterior to the jaw or mandibular segment, and anterior to the commissure of the jaw or mandibular segment, he finds another one which he considers to be the first postoral commissure. His theories have been supported by Weber (1952) who says in his discussion of Henry's and Pflugfelder's papers, "It [Henry's opinion that the mandibular nerve belongs to the tritocerebrum] . . . is nevertheless erroneous and Pflugfelder refuted Miss Henry's opinions in advance without having known her work published at the same time as his."

Despite these opinions of Pflugfelder that appear to support Federov, and Weber's acceptance of the idea that a premandibular somite exists in the Onychophora, there are several factors that one must consider before accepting Pflugfelder's work. In the first place in the stages preceding the formation of the preoral cavity one may plainly see that the feeding claws are the appendages of the segment immediately behind the antennal segment (fig. 5 A, B, C), that they are adjacent to the second ventral organs, and that there is no extra coelomic sac between the segments of the antennae and of the feeding claws (fig. 4 D).

It is evident that Pflugfelder used an advanced embryo of *Paraperipatus amboinensis* in making the series of cross sections upon which he based his conclusions. The preoral cavity has formed and the feed-

ing claws have withdrawn into this cavity. Also a cephalic movement, accompanied by a dorsal movement, of the ventral organs around the stomodaeum has commenced. This leads to alterations in position and even to distortion of the ventral organs involved. I, therefore, feel that placing full reliance upon such sections is not justified.

Pflugfelder's efforts to prove the presence of a premandibular segment would be more acceptable if he had found such a segment at an earlier stage before the preoral cavity had begun to form.

Both Pflugfelder and Federov apparently base their theory of head segmentation in the Onychophora on the assumption that the feeding claws are true mandibles, and the necessity to interpolate another segment between the antennal and the mandibular segments has led them into complicated reasoning that is hard to follow. The earliest stages in which segmentation appears have always been accepted as the stages that determine segmentation in any form, and the Onychophora should not be considered as exceptions to this rule.

SUMMARY

The head of *Peripatus* is an undifferentiated region without grooves to mark its segmental areas. The head appendages are the antennae, the feeding claws, and the slime papillae. There is no labrum, the preoral cavity being surrounded by oral lobes constituting the lips, the dorsal lobe of this group forming a structure similar to the epipharynx of insects. The dorsal lobe aids in the ingestion of food. The feeding claws are not homologous with mandibles but rather correspond to the transitory labral lobes found in some insect embryos. This is indicated by the following facts:

1. They are innervated by the third or tritocerebral segment of the brain.

2. They do not function as mandibles or chewing jaws but more as scratching claws.

3. The coelomic sacs of the feeding claw segment are located immediately behind the antennal coelomic sacs.

4. The ventral organs of the feeding claw segment form the third or tritocerebral lobes of the brain.

5. The feeding claws do not form from ental lobes of the basal leg segments as in insects, but are simply greatly strengthened claws developed from a much altered walking leg.

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